TEMPORAL AND SPATIAL VARIATION IN SEX RATIO AND MATING FREQUENCY IN SOLDIER BEETLES[1]

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Abstract.—Previous studies of the mating system of the soldier beetle, *Chauliognathus pennsylvanicus,* have not considered spatial or temporal variation in sex ratio or the relative frequency of mating and single adults. These two attributes of the mating system were sampled at mid-day and again in the early evening thrice weekly throughout one adult flight season at two localities in Tennessee. Sex ratios were equivalent within days but became increasingly male biased as the season progressed. The proportion of all adults found copulating is about 5 times greater in the early evening than at mid-day. Some between-site differences were found.

The soldier beetle, *Chauliognathus pennsylvanicus* (Coleoptera: Cantharidae), is one of the most common old field insects in the eastern United States during late summer and early autumn. A number of studies have examined mating behavior as it relates to the operation of sexual selection in natural populations of this beetle (Mason, 1972; McCauley and Wade, 1978; Mason, 1980; McCauley, 1981; McLain, 1981; Woodhead, 1981; McLain, 1982). Most of these studies have focused on identifying those characteristics of individuals that determine the probability of being found in copula when a random sample of single and mating adults is taken from a field population. Body size, antennal morphology, population density, presence or absence of interspecific competitors, and female reproductive status have all been shown to influence the probability that an individual will be found mating.

The published studies of the *Chauliognathus* mating system are based on short term observations. Typically, several collections are made at mid-day several days apart. Any temporal or spatial variation in attributes of the mating system such as the operational sex ratio or female receptivity that would be likely to affect the process of mate selection would go undetected when data is taken in such a fashion. It is unknown whether the mate selection process varies with time of day, between days, or from locality to locality. A more complete assessment of the *Chaulignathus* mating system would require knowledge of any such variation. The present study describes one full season of mating activity of the beetles and analyzes daily and seasonal variation in operational sex ratios and the frequency of mating in two natural populations of *C. pennsylvanicus* located in middle Tennessee.

MATERIALS AND METHODS

The two study sites (A and B) in Davidson County, Tennessee were selected such that their close proximity ensured nearly identical weather conditions on any given census day. While field A was considerably larger than field B, they were similar in the relative abundances and phenologies of the numerically dominant plants. Adult
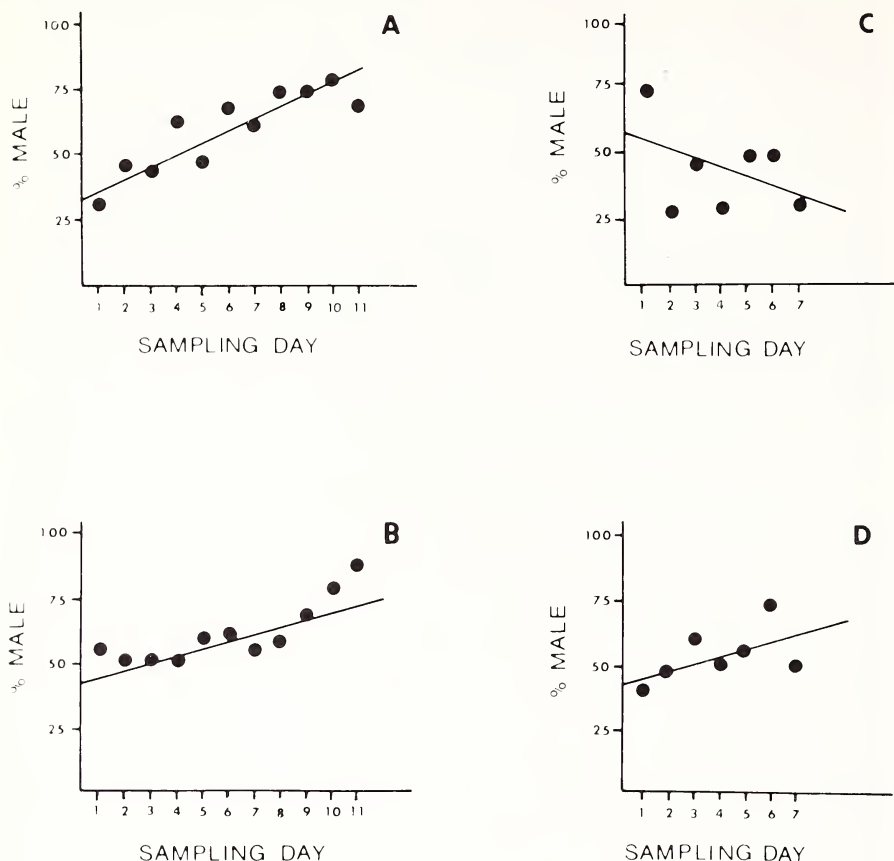
Fig. 1 (A–D).   Percent males represented in samples of adult *Chauliognathus pennsylvanicus* taken: A) at study site A at mid-day, B) at site A in the evening, C) at site B at mid-day, and D) at site B in the evening. Least squares regression equations of percent males on (Y) sampling day (X) are: A) $Y = 32.5 + 4.4X$; B) $Y = 43.4 + 2.8X$; C) $Y = 55.9 - 2.8X$; D) $Y = 42.9 + 2.8X$.

soldier beetles are pollen feeders and mate at the feeding sites. Goldenrod (*Solidago* spp.) provided the primary food resource at the beginning of the study in September and was gradually replaced in October by an aster (*Helianthus* sp.). Adult sex ratio and percentage adults seen in copula were censused at each site. In Field A (the larger field) the first 200 beetles encountered in a random transect of the field were sexed and categorized as either "mating" or "solitary." The same procedure was applied to the first 100 beetles observed in Field B. Care was taken at both sites to look for beetles throughout the vegetation (not just on the flowerheads where they tend to aggregate) in order to prevent sampling bias in the sex ratios.

The populations of *Chauliognathus* were sampled during three mid-day surveys (11:00 A.M.–1:00 P.M.) and three late afternoon surveys (5:00–7:00 P.M.) each week
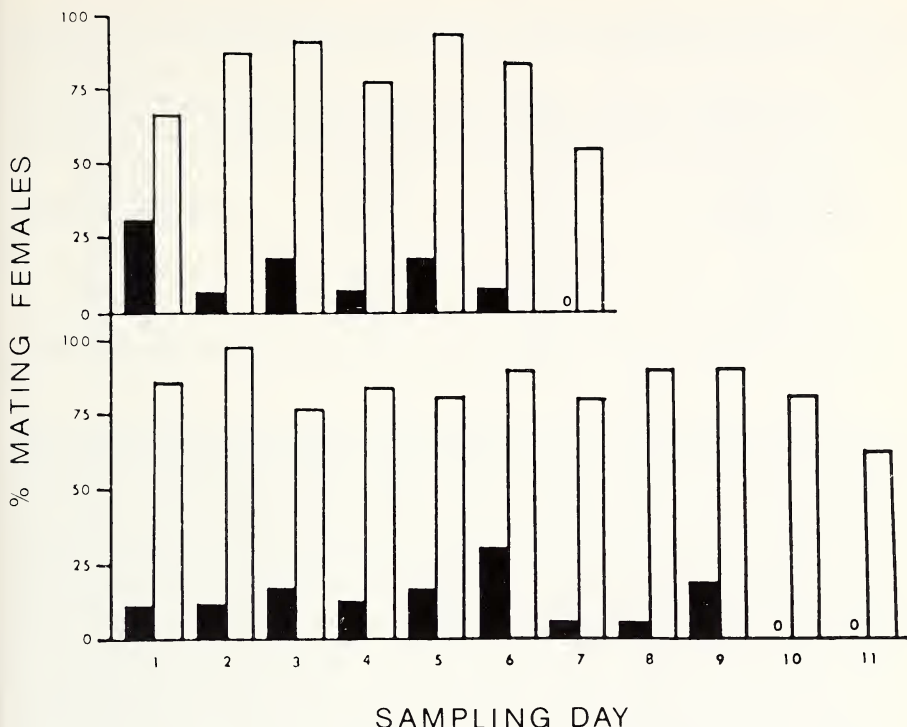
Fig. 2.   Percent of sampled females found mating at study sites B (top) and A (bottom). Dark bars represent mid-day samples; open bars evening samples.

beginning September 13, 1982. Field A was sampled until October 18; Field B until October 4. Surveys were terminated at each site when adult beetles became very rare or non-existent. When mid-day and late afternoon surveys could not be taken on the same day, surveys taken on successive days were paired to facilitate temporal and spatial comparisons.

RESULTS

The operational sex ratios estimated at the 2 study sites are presented in Figure 1 (A–D). At study site A the sex ratios became increasingly male biased as the season progressed. Linear regression of percent males on time reveals this trend to be statistically significant for both the mid-day ($P < 0.01$) and evening samples ($P < 0.05$). At study site B no such trend can be documented statistically ($P > 0.10$ in both cases). The 4 regression lines were compared with respect to the equality of their slopes and found to be highly heterogeneous ($P < 0.001$). There appears to be a real difference between localities in temporal trends in the sex ratios. Testing of individual samples for a goodness of fit to a 50:50 sex ratio reveals that not only are later samples at site A significantly male biased but that the mid-day samples are actually slightly

Table 1.   Three factor analysis of variance of the percent of sampled females found mating. With one replicate per treatment cell the A × B × C interaction term serves as the error mean squares.

Source of variation	df	M.S.	F	
Location, A	1	0.040	3.64	N.S.
Sample day, B	8	0.011	1.00	N.S.
Time of day, C	1	4.310	398.80	$P < 0.001$
A × B	8	0.011	1.00	N.S.
A × C	1	0.010	0.91	N.S.
B × C	8	0.050	4.55	N.S.
A × B × C	8	0.011		

female biased at the onset of the adult flight season. As a group, the goodness of fit G tests are highly heterogeneous as would be expected from the results of the regression analysis.

Given that sex ratios are male biased, at least some of the time, a study of temporal variation in mating frequency requires that the proportion of males found mating be analyzed separately from that of females. The proportions of females found to be mating at the various censuses is presented in Figure 2. It is obvious that far more females can be found mating in the early evening than at mid-day. The data were analyzed by a three-factor analysis of variance in which the 3 factors were time of day, day of season, and locality. Only time of day was found to be statistically significant (Table 1). Pooling results across census days and fields, it was shown that, on average, 13.2 percent of the adult females are mating at mid-day compared to 84.3 percent in the evening. A similar analysis of the proportion of males found mating reveals that in addition to the highly significant effect of time of day, the day of the season also has an effect (Table 2). This is not surprising given the observations made on the sex ratio.

DISCUSSION

Despite the large number of studies of mate selection in *C. pennsylvanicus,* little is known about those characteristics of its natural history and reproductive physiology relevant to a more complete description of its mating system. Male biased sex ratios have been shown previously (Wiener, 1974; Brown and Brown, 1984) but the extent of the temporal trend in variation in the sex ratio has not been previously documented. The mechanism by which populations become increasingly male biased is not clear since these studies were not designed to partition sex-specific mortality effects from emigration. Females could have a shorter life expectancy than males or they could disperse from the old fields prior to oviposition. That sex ratios are not male biased at all localities and are not male biased at the onset of the breeding season suggests that the male bias does not result from unequal sex ratios at birth nor from differential survivorship during the larval period. Whatever the mechanism, seasonal changes in the operational sex ratio would be expected to exert an influence on the mating system, probably intensifying competition among males for mates.

Table 2. Three factor analysis of variance of the percent of sampled males found to be mating. With one replicate per treatment cell the A × B × C interaction term serves as the error mean squares.

Source of variation	df	M.S.	F	
Location, A	1	0.00	0.00	N.S.
Sample day, B	8	0.04	3.64	$P < 0.05$
Time of day, C	1	2.70	245.45	$P < 0.001$
A × B	8	0.01	0.91	N.S.
A × C	1	0.01	0.91	N.S.
B × C	8	0.03	2.73	N.S.
A × B × C	8	0.01		

It is also not clear what generates the daily cycle in the proportion of the population found to be mating. Behavioral observations by McCauley and Wade (1978) suggest that males will attempt to copulate with nearly any single female that they encounter. Most females resist copulating with males, at least until the male has succeeded in subduing the female with antennal stroking. Woodhead (1981) has shown that a female's receptivity seems to be predicted by the maturity of her eggs, at least at mid-day. It would seem that female receptivity must further change with the time of day, perhaps as a function of ambient temperature or incidental light. Depending on the frequency and timing of oviposition and the manner in which sperm is transferred and utilized, the success of a male of a given body size at mating at mid-day could be a poor predictor of his overall reproductive success.

This paper is not intended to discredit those previous short term studies of *C. pennsylvanicus* but rather to add to them by pointing out that temporal variation in some rather obvious populational parameters could greatly influence our interpretation of the mating system and what determines a fit male.

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